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LATITUDINAL GRADIENTS IN SPECIES DIVERSITY OF THE NEW WORLD SWALLOWTAIL BUTTERFLIES

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It has long been realized that many taxa are represented by more species in the tropics than at higher (especially northern) latitudes (Wallace, 1878). Butterflies (Hovanitz, 1958), dragonflies (Kennedy, 1928), trees (Dobzhansky, 1950; Cain and Castro, 1959), mammals (Simpson, 1964), birds (MacArthur, 1964; Karr, 1971), snakes, lizards and other groups (Fischer, 1960) follow this broad trend of increasing species diversity from northern latitudes toward the tropics. Although recent studies have greatly expanded our understanding of the causes of high diversity in tropical areas (Connell and Orias, 1964; Pianka, 1966; Saunders, 1968; MacArthur, 1969; Karr, 1971; and others), there seems to be no general explanation for all increased tropical diversities, and the importance of the various causes may vary with the taxa being studied. In the present paper latitudinal gradients in species diversity are examined for a particular group of butterflies. An attempt is then made to interpret the factors which contribute to the observed patterns and to fit these factors into an acceptable theory.

The group chosen is the New World swallowtail butterflies of the subfamily Papilioninae, family Papilionidae. An advantage of studying this group of herbivores over many others is that the geographical ranges of the adults and the feeding habits of the larvae are reasonably well known (Edwards, 1868-1897, 1889; Reed, 1877; Burmeister, 1879; Gundlach, 1881; Scudder, 1889; Rothschild and Jordan, 1906; Silva, 1907; D'Almeida, 1922, 1966; Jordan, 1924; Dethier, 1940; Bourquin, 1944; Wolcott, 1948;

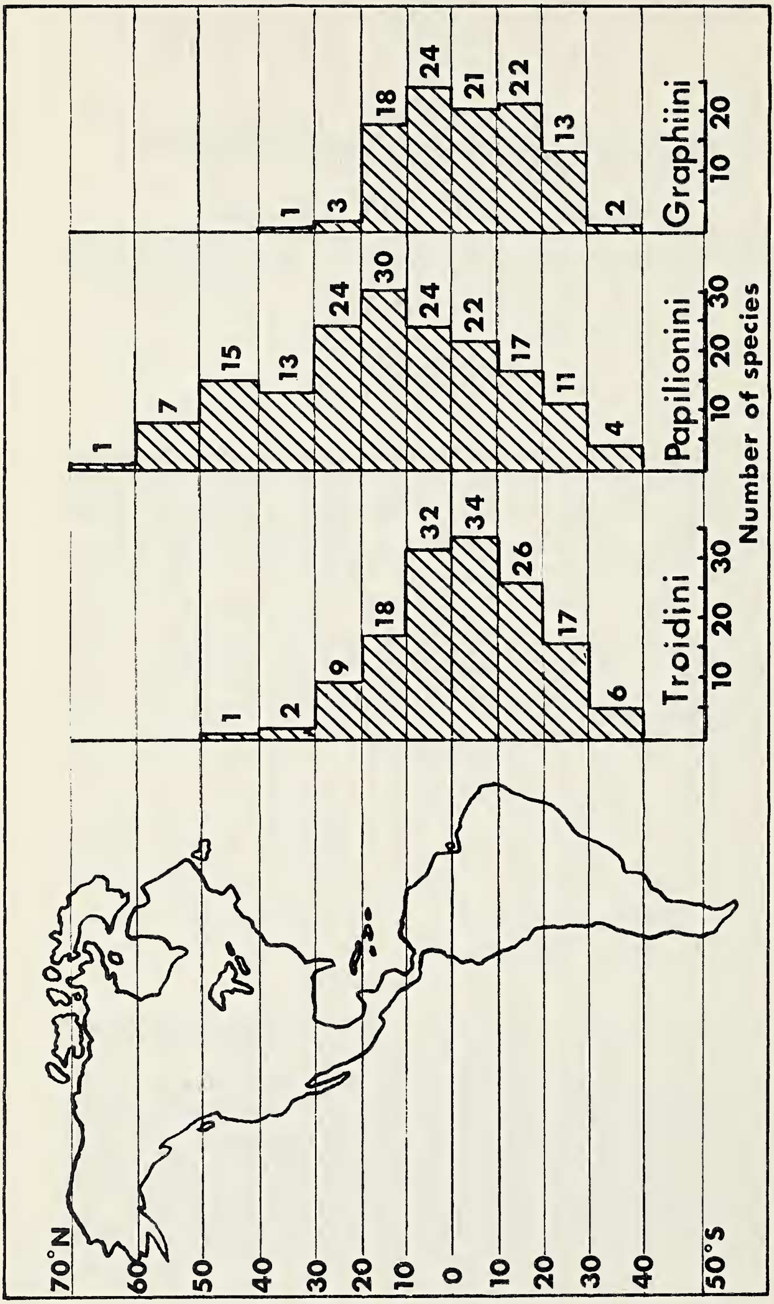

Fig. 1. - Map of New World showing latitudinal gradients in numbers of species of three tribes of swallowtail butterflies.

Bauer, 1955; Pronin, 1955; Biezanko, 1959; Brower, 1959; Klots, 1960; Munroe, 1960; Ehrlich and Ehrlich, 1961; Brooks, 1962; Newcomer, 1964; Ross, 1964a,b; Ehrlich and Raven, 1965; Brown and Mielke, 1967a,b; Costa Lima, 1968; Perkins, Perkins, and Shininger, 1968; Holland, 1969). There are approximately 175 species of Papilioninae in the New World which are divided into three tribes on the basis of adult morphology, structure and food-plant associations of the larvae, pupal morphology, and geographic distribution (Munroe, 1960; Munroe and Ehrlich, 1960). These are the Troidini (about 60 species), the Papilionini (about 65 species), and the Graphiini (about 50 species).

METHODS

Measurement of species diversity

Sophisticated measures of diversity of species within natural communities have been developed in recent years (see Pianka, 1966; Pielou, 1969; Whittaker, 1970a; and references therein). Because such measures generally require knowledge of the relative abundances of the component species, and because such data for the swallowtails are lacking, diversity is here represented simply as the number of species per latitudinal belt, arbitrarily chosen to be 10° latitude in width.

Swallowtail ranges and food-plant records

Data on the geographical ranges of the swallowtails were taken primarily from Rothschild and Jordan (1906). Since 1906 about twelve new species have been described and these are included in the present discussion where their ranges are known. In the few cases where two or more species have been synonomized (Munroe, 1960), their ranges have been combined.

Latitudinal ranges were represented graphically in terms of the presence or absence of a species within successive latitudinal belts. Ranges were assumed to be continuous from the northernmost record to the southernmost record of collection, a reasonable assumption except perhaps for a few, extremely wide-ranging species. The numerous maps of individual species ranges are not included here for reasons of spatial economy. The graphic representation of these ranges implies both a static temporal and spatial distribution. However, apart from obvious seasonal fluctuations and migrations, the ranges of these butterflies may be expanding or contracting, either naturally or more likely through man's activities.

TABLE 1

Distribution of larval food-plant families and of swallowtails feeding upon these plants. Most important families are underlined.

Tribe	Distribution	Food-plant family	Distribution	References to plant distributions
Troidini	Mainly 20° N to 30° S latitude	Aristolochiaceae, Rutaceae	Ari.: mainly tropical, fewer than 20 sp. in U.S. and Canada; 80 sp. in Brazil and surrounding countries. Rut.: mainly subtrop. and trop.	Planchon, 1891; Patterson, 1892; Hoehne, 1927; Fernald, 1950.
	Most between 30° N and 30° S latitude	Rutaceae, Berberidaceae, Lauraceae, Piperaceae	Rut.: mainly subtrop. and trop., fewer than 20 of some 400 New World sp. in U.S. Commercial citrus between 35°N and 35°S lat. Ber.: north temperate and mount. S.A. Lau., Pip.: mainly subtrop. and trop.	Patterson, 1892; Record and Hess, 1940, 1942; Fernald, 1950; Trelease and Yuncker, 1950; Yuncker, 1953; Hutchinson, 1959; Bernardi, 1962; Reuther, Webber, and Batchelor, 1967.
Papilionini	Mainly north of 30° N latitude	Umbelliferae, Compositae (Artemisia)	Umb.: mainly temp., 250 sp. in N.A., 50 sp. in Mexico, few in trop. S.A., mostly in mount. regions, 50 sp. in southwestern S.A. Com. (Artemisia): north temp. and southern S.A.	Coulter and Rose, 1888; Patterson, 1892; Britton and Brown, 1913; Dethier, 1941; Mathias and Constance, 1950, 1967; Good, 1953; Matuda, 1958.
	Most north of 30° N latitude	Corylaceae, Lauraceae, Magnoliaceae, Oleaceae, Rosaceae, Rutaceae, Betulaceae, Platanaceae Rhamnaceae, Salicaceae Saxifragaceae	Mostly north temp.: Bet., Cor., Mag., Ole., Pla., Ros., Sal. Subtrop. and trop.: Lau., Rut. Rha.: temp. and warm regions. Sax.: mainly cold and temp. regions.	Britton and Brown, 1913; Good, 1925; Hutchinson, 1959, 1964, 1967; Brockman, 1968.
Graphiini	Mainly 20° N to 30° S latitude	Annonaceae, Lauraceae Magnoliaceae, Verbenaceae	Ann.: mainly trop., less than 10 sp. in U.S., 600 sp. from Mexico to southern Brazil and northern Argentina, few further south. Lau., Ver.: subtrop. and trop. Mag.: north temp.	Patterson, 1892; Fries, 1930, 1931, 1934, 1937, 1939; Fernald, 1950; VanderWyk and Canright, 1956; Hutchinson, 1959.

Food-plant records were extracted largely from Ehrlich and Raven (1965) and references therein. Where other sources were consulted, food-plant records were evaluated with considerable caution (Shields, Emmel, and Breedlove, 1969).

RESULTS AND DISCUSSION

A map of the New World showing the latitudinal gradients in species diversity for the three tribes of swallowtail butterflies is represented in Figure 1. It is clear that the New World Papilioninae exhibits a latitudinal gradient of increasing species diversity, with the number of species increasing from the high northern latitudes (one species between 60° and 70° N latitude) to the tropics (149 species between 20° N and 20° S latitude) and then decreasing southward (12 species between 30° and 40° S latitude). The three tribes exhibit this gradient to varying degrees: the Troidini and Graphiini are restricted mostly to tropical and subtropical regions; the Papilionini has the widest and most northern distribution.

The distribution of the main larval food-plant families and of the swallowtails feeding upon these plants are given in Table 1. It can be seen that the greatest diversities of the swallowtail butterflies are in the areas where their main larval food-plant families are apparently most diverse in terms of numbers of species, and that these areas, for many of the main food-plant families, are the tropical and subtropical regions.

Two questions merit further discussion. What factors limit the northernmost and southernmost distributions of these swallowtail butterflies? And what factors are responsible for the observed increased tropical diversity of these swallowtail butterflies?

Limiting factors in the north

The northernmost range of insects in general is clearly limited by the physiological effects of low temperature. In addition a low annual heat budget, severe and often variable weather, and the continuous light of the short growing season affect both insects and plants, but apparently the decrease in insect species is greater and probably somewhat independent of the reduction in plant species (Downes, 1964). Only *Papilio machaon*, and Umbelliferae-feeder, is found north of 60° N latitude where at least three other possible swallowtail food-plant families are represented (i.e., Betulaceae, Compositae, and Salicaceae; Hanson, 1953). The few butterfly species found in the Arctic usually have increased melanism and hairiness, which, together with the habit of basking, allow them to absorb solar radiation and achieve the body temperature necessary for flight (Downes, 1964; Watt, 1968).

Downes (1964, p. 279) concluded:

> The arctic is not inherently simple and does not forbid a greater diversity, yet in fact very few species occur. . . . the arctic will always tend to lie towards the limit of the physiologically possible range because in fact the greatest continuity of evolutionary history has been in the tropics and most forms of life have thus been shaped in response to tropical conditions.

Limiting factors in the south

None of the species considered here is known to extend south of 40° S latitude. All but one species found at this southern limit of distribution mainly follow the tropical rain forest climate southward through eastern Brazil and into the permanently humid grassland climate of eastern Uruguay and northeastern Argentina where broadleaf evergreen and deciduous trees break up into patches surrounded by grass and other herbaceous plants (Kuchler, 1952). Further south the pampas merge into the arid, sterile plains of Patagonia, where only scanty vegetation grows in stony, exposed, and excessively dry conditions (Campbell, 1944).

The only other species found south of 30° S latitude is apparently isolated in the vicinity of Valparaiso (western Chile) by the Andes to the east and the practically rainless and barren Atacama desert to the north, a region which has been called "one of the driest, least fertile areas in the world" (Good, 1933). Rainfall is greater in west central Chile and somewhat further south, and a broadleaf evergreen and deciduous rain forest is present (Good, 1933; Kuchler, 1952). Although there is little similarity to the Arctic zone of the Northern Hemisphere, this southwestern rain forest gives way to a sub-Antarctic flora further south (Campbell, 1944). Aside from a few microlepidoptera, southern Chile is lacking in moths and butterflies (Kuschel, 1960).

Darlington (1965) cited many instances of numbers of species decreasing from central to southern South America. As an explanation of this decrease he suggested the increase in intensity toward the south of such factors as cold, alteration of seasons, shortness of days in winter, and lack of warmth in summer. Thus, while in the extreme south low temperature seems to be the major limiting factor in insect distribution, it appears that lack of moisture and the resulting scarcity of vegetation are the factors limiting the southward distribution of the swallowtails. Although a favorable area exists in west central Chile, these butterflies are hindered from entering it by the hot northern Chilean desert, the cold southern Argentinean desert, and the Andes mountains surrounding it.

Tropical diversity

Certainly the greater vegetational diversity in the tropics creates a greater variety of food for the swallowtails, but this greater vegetational diversity is only a proximate explanation, as Simpson (1964) has pointed out. In other words, given that the Umbelliferae-feeders are more diverse in regions where the Umbelliferae is more diverse, and that the Aristolochiaceae-feeders are more diverse in regions where the Aristolochiaceae is more diverse, the question remains as to why there are not 60 or 70 species of Umbelliferae-feeders (instead of 10 to 15) with some 250 species of Umbelliferae available in the north temperate zone, and why there are not only 10 or 15 species of Aristolochiaceae-feeders (instead of some 60) with only about 80 species of Aristolochiaceae present in the New World tropics.

Part of the answer becomes apparent when the evolutionary history of the Papilionidae is examined. Based upon various lines of evidence it is believed that the butterflies in this family evolved and diversified in tropical areas on Aristolochiaceae and that as they spread into regions where this plant family was not well represented or absent, they exploited other plant families chemically similar to the Aristolochiaceae (Munroe and Ehrlich, 1960; Ehrlich and Raven, 1965). Many species in the Graphiini and Papilionini feed upon Annonaceae, Lauraceae, and Magnoliaceae, which, in addition to some other plant families, form a closely allied group in the order Ranales (Ehrlich and Raven, 1965) (i.e., Magnoliales; Cronquist, 1968). The Aristolochiaceae and families in the Magnoliales share some similar alkaloids (Alston and Turner, 1963; Hegnauer, 1963), and are apparently closely related in certain morphological structures as well (Thorne, 1963). A few Aristolochiaceae-feeders and many species in the Papilionini feed upon Rutaceae, a family containing some alkaloids in common with familes in the Magnoliales, as well as other alkaloids (Hegnauer, 1963; Price, 1963). Some families in the Magnoliales (e.g. Magnoliaceae and Lauraceae), the Rutaceae, and the Piperaceae all have some species which contain various essential oils in common with the Umbelliferae

(Dethier, 1941). Cyanogenic, phenolic and other glycosides are found in Betulaceae, Oleaceae, Salicaceae, and Rosaceae (Paris, 1963), all of which are larval food-plants for some species in the Papilionini. From the feeding relationships of these three tribes of swallowtails and the chemical relationships among the food-plant families it is apparent that the swallowtails feed upon a number of chemically, if not taxonomically, related plants. In fact, the food-plant preferences of many insects are apparently of a chemical nature, dependent upon the secondary chemical content of the plants (Fraenkel, 1959; Dethier, 1970; Whittaker and Feeny, 1971).

On the basis of the distribution of certain of these compounds and the feeding habits of various species in the Papilionini, a gradual transition in feeding habits from the Rutaceae (containing alkaloids) through intermediate food-plants (with varous combinations of alkaloids and essential oils) to the Umbelliferae and a few chemically related Compositae (i.e. *Artemisia*) (containing essential oils) has been suggested (Dethier, 1941). A more abrupt transition might also have occurred as certain facultatively polyphagous papilionid larvae (i.e. larvae 'normally' feeding on a particular plant but able to feed and survive on certain other plants if given the opportunity) exploited ovipositional variability in adult females by surviving on the 'abnormal' food-plant and produced adults which generally prefer to oviposit on the new food-plant (Stride and Straatman, 1962; see also Hovanitz, 1969).

The Umbelliferae-feeders, in changing their feeding habits from the rest of the Papilionini, chose a family of plants characteristic of temperate areas. The Umbelliferae is apparently more recently evolved than the Aristolochiaceae (Cronquist, 1968), and thus its swallowtail fauna may not yet have had enough time to reach maturity or saturation (e.g. Southwood, 1961) as evidenced perhaps by the fact that the Umbelliferae-feeders are restricted mainly to plants in only one of three subfamilies in the Umbelliferae (Ehrlich and Raven, 1965).

Another factor apparently involved in the increased tropical diversity exhibited by these butterflies is the relatively predictable, favorable climate of much of the New World tropics. From approximately 20° N to 20° S latitude at low altitudes there is no frost, monthly rainfall variability is less than 20% of the mean, the maximum annual temperature range is usually much less than 30° F, and the average daily temperature range is usually greater than the average annual temperature range.

Although this is a broad generalization subject to considerable exceptions, these factors qualify this area as one of "maximum climatic stability" (Klopfer and MacArthur, 1961).

A number of important considerations arise from this generalization: 1) Evolution in general is usually considered to be faster in the tropics than in other areas (Dobzhansky, 1950; Darlington, 1959) and this might particularly be expected to be true for the evolution of insects. Insects, being poikilothermic, are directly dependent upon the external temperature and a warmer, more favorable temperature for a longer period of time might be expected to increase mutation rate and the number of generations per year and thus increase the appearance of favorable mutations and gene complexes (De La Rue, Bourliere, and Harroy, 1957; Carcasson, 1964; Stehli, Douglas, and Newell, 1969). While evidence of increased tropical mutation rates is lacking, it has been known for a long time that larval development in insects may be facilitated by increased temperature (Dimmock, 1888) and it is common for many butterflies to exhibit one or more additional broods in the southern parts of their ranges than in the northern parts (Klots, 1960). Although some of the swallowtails reported here, including both those found in the region of climatic stability and those found outside it, breed all year long, brood following brood, many also exhibit predictable, seasonal-like variations, especially in regard to changes in rainfall. These periods of abundance and scarcity of the swallowtails are undoubtedly often due to corresponding periods of abundance and scarcity of the larval food-plants (such as occurs in temperate regions) but they also occur in some species even though larval food-plants continue to be present, perhaps being due to changes in the availability of adult food sources (Rothschild and Jordan, 1906; Wiltshire, 1959; D' Almeida, 1966; Emmel and Leck, 1969; M. Barcant, K. S. Brown, A. Cardoso, G. Kesselring, M. Serrano, T. Turner, personal letters). Thus no generalization regarding an increase in the number of generations and hence a supposed increased rate of evolution of the swallowtails in the region of climatic stability is possible.

The year long favorable climate does however allow a high number of swallowtail species to be found at any month of the year, while the cold months of the north temperate zone and the dry months of the south temperate zone prevent most swallowtails from flying during these harsh times (Table 2). This factor may be causally related to the increased tropical diversity observed in these swallowtails but its actual implications are not clear.

2) Local animal diversity is in some cases directly related to the number of predators in the system because these prevent any one species from monopolizing a limited resource and thus allow more species to coexist. Areas with increased stability of annual production, such as the tropics, are apparently able to support more predators and consequently be more diverse (Paine, 1966). Although data on swallowtail predation are practically non-existent, one might expect that predation in the tropics, of adults at least, is an important factor because of the existence of a great number of mimicry complexes (Rothschild and Jordan, 1906; Sheppard, 1961; Blest, 1966; Wickler, 1968). This apparent increased predation pressure may thus contribute to the increased tropical diversity of these swallowtails.

3) Species coexisting in a habitat apparently can be more similar if productivity is high, if individual species abundances are low (apparently true for tropical butterflies in general; Ebert, 1969), and if the seasons are relatively uniform (MacArthur, 1965), factors which generally describe much of the tropics. Niches apparently can be narrower in stable communities (MacArthur, 1955), and it has been mathematically determined that if niches are narrower, more species can coexist in a given environmental range (MacArthur and Levins, 1967).

TABLE 2

Number of swallowtails flying at each month of the year in the region of climatic stability (CS), in the area north of this region (NCS), and in the area south of this region (SCS)*

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
CS	38	28	32	29	31	43	41	38	31	30	25	30
NCS	2	3	5	7	12	14	13	9	7	6	2	2
SCS	10	11	6	2	0	1	2	7	7	11	11	11

* Data for CS based on 77 species (about 67% of the total species found in that region); for NCS, 18 species (about 50%); and for SCS, 13 species (about 52%). Data compiled primarily from Rothschild and Jordan (1906).

For the swallowtails, data on one aspect of their niche, food-plant preferences, are available for study. It appears that the relatively general feeders (broad niche) are more prevalent in the north temperate zone (Table 1), probably because the advantage in a changeable climate lies with the general feeder that can switch to an alternate food-plant if its primary one is not available due to the vagaries of the climate. In the tropics, the butterflies can apparently specialize more (narrow niche) because they are more or less guaranteed the presence of their particular food-plant due to the favorable, relatively predictable climate. While this fits in well with the above mentioned theoretical considerations, at least two problems arise. One is that although there are a number of relatively general feeders in the north temperate zone, these feed primarily upon deciduous trees and shrubs, a rather stable and reliable food source when compared with short-lived annual herbs. The other is that due to the chemical nature of food-plant preferences, most butterflies are restricted in their choice of food-plants, usually to plants in one or two chemically related plant families, and even the relatively general feeders appear to show particular preferences in different parts of their ranges (Brues, 1920; J. M. Scriber, personal communication).

However, data on these swallowtails' ability to switch food-plants if necessary are lacking. Organisms in harsh regions (i.e. physically stressed and unpredictable environments) apparently maintain a high degree of genetic variability and consequently utilize a larger share of the resources than organisms living in favorable regions (i.e. stable and predictable environments) where genetic variability would be selected against because the disadvantages of a high genetic load would outweigh the advantages of high genetic flexibility in these more stable environments (Grassle, 1967). Thus it may be that temperate species are more 'plastic' in food habits than tropical species. Of course, many other factors are involved in determining a species' niche, and it appears that the contribution of this factor of niche breadth to the increased diversity of the tropical swallowtails is significant. Research to compare niche breadth in temperate and tropical swallowtails is currently underway in our laboratory.

The factors discussed above fit in well with the stability-time hypothesis developed by Saunders (1968) to account for increased tropical diversities. In physiologically harsh areas (harsh due to unfavorable physical conditions and increased physical fluctuations) organisms apparently must utilize a major portion of their energy budget for coping with the physiological stresses, but in favorable areas (favorable due to reduction in harsh physical conditions and in physical fluctuations), organisms are apparently subjected to increased biotic stresses (e.g. competition and predation) such that a major portion of their energy budget is utilized in the coevolution of complex communities (see also Karr, 1971).

Thus what appears to have happened is a synergistic coevolution of plant-herbivore interactions, accentuated by the abundance of phytophagous insects in physiologically favorable tropical regions and resulting in increased diversity of both plants and herbivores (Brues, 1920; Gillett, 1962; Ehrlich and Raven, 1965). The fact that these interactions are basically of a chemical nature implies that, unlike bird diversity which apparently depends primarily upon the structure of the community and broad food categories and thus becomes saturated (MacArthur, 1964; 1969), unlimited possibilities exist for the continued increase in terrestrial plant and insect diversities (Whittaker, 1969; 1970b), provided man radically and rapidly alters his policy of worldwide environmental destruction.

SUMMARY

Latitudinal gradients in species diversity are examined for the New World swallowtail butterflies in the subfamily Papilioninae, family Papilionidae. Species diversity is measured as the number of species present per 10° latitudinal belt, determined from the literature. The three tribes in the Papilioninae (the Troidini, the Papilionini, and the Graphiini) are shown to exhibit to varying degrees a pattern of increasing species diversity from high northern latitudes (one species between 60° and 70° N latitude) to the tropics (149 species between 20° N and 20° S latitude) and then decreasing southward (12 species between 30° and 40° S latitude). It is also shown that these swallowtail butterflies are most diverse in areas where their main larval food-plant families appear most diverse.

Factors limiting the general overall distribution of these swallowtails are interpreted to be mainly the adverse effects of low temperature in the north and the lack of moisture and resulting scarcity of vegetation in the south. Factors which are considered important in their contribution to the increased tropical diversity of the swallowtails include: 1) the diversity of the main larval food-plants, which for many of the main food-plant families (i.e. Aristolochiaceae, Annonaceae, and Rutaceae)

is greatest in subtropical and tropical areas; 2) the evolutionary history of the Papilionidae, the primitive stock of which apparently evolved and diversified in tropical areas; and 3) the predictable, favorable climate of much of the tropics, which allows a high number of swallowtail species to be found at any month of the year. This favorable climate apparently also allows increased predation pressure as evidenced by the great number of mimicry complexes in tropical butterflies and probably allows increased similarity and specialization of the tropical swallowtails. These factors are intermeshed in the synergistic coevolution of plants and herbivores, mainly on a chemical level, which has resulted in the more complex communities of these tropical areas.

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